



The social organization of the Mandarin vole, *Lasiopodomys mandarinus*, during the reproductive period

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Receipt of Ms. 20. 04. 1999

Acceptance of Ms. 14. 07. 1999

Abstract

The social system in a free-living population of the mandarin vole *Lasiopodomys mandarinus* was examined in Selenginski District, Buryatia, by use of the mark-capture method. Mandarin voles lived in extended family groups. The members of the group occupied a common burrow and were strongly attached to it. The summer groups consisted of one breeding male, 1–5 breeding females, and young of 1–3 generations with a mean of 8.7 (range 3–22) individuals per burrow. Most of the offspring remained within the natal territory at least up to 50 days. None of the 72 young males and only three of the 73 young females became reproductive while staying in natal burrows. The change of sire appears to be the necessary condition for the reproductive activation of philopatric daughters.

Thus, *L. mandarinus* exhibits a high level of sociality based on communal breeding, prolonged pair-bonding and parent-young relationships. This set of traits is also reported in the literature for *Lasiopodomys brandtii*. It is suggested that sociality was characteristic of ancestral above ground form and represented the precondition to occupy the recent niche of the fossorial stenophage.

Key words: *Lasiopodomys mandarinus*, mating system, philopatry, territoriality, subterranean rodents

Introduction

The mandarin vole *Lasiopodomys mandarinus* inhabits the grasslands of China, Korea, North Mongolia, and the borderland in the south of the Transbaical region of Russia. Very little is known about its habits. Meanwhile, scanty information from the works of former authors (FETISOV 1955; HYAN-VAN-DI 1960) and especially the recent studies in the Mongolia and Transbaical region (DMITRIEV 1980; SMORKATCHEVA et al. 1990) characterise *Lasiopodomys mandarinus* as an extremely interesting aberrant form.

Apparently, throughout its range *L. mandarinus* leads an almost completely subterranean existence. Its burrows are extensive: the number of entrances is up to 50–70 and the tunnels are up to 95 m long. Most of the tunnels are close to the surface and serve to forage underground for roots and tubers. In Mongolia and Buryatia the mandarin vole feeds almost entirely on *Stellera chamaejasme* using both its massive roots and green parts (DMITRIEV 1980; SMORKATCHEVA et al. 1990). Even when foraging for stems and leaves of *Stellera*, voles rarely go away more than 0.5–1 m from a burrow entrance which usually is near this plant (SMORKATCHEVA et al. 1990).

The reproductive period lasts in the Transbaical region at least from early April through late August. Winter breeding is likely although there is an autumn break (SMORKATCHEVA et al. 1990; SMORKATCHEVA 1993). Unlike most voles of grasslands – e.g. *Lasio-*

podomys brandti, *Microtus socialis*, *M. arvalis*, *M. gregalis*, *M. ochrogaster* (SVIRIDENKO 1934; KHRUSTZELEVSKI 1954b; TAITT and KREBS 1985; GETZ et al. 1987) – *L. mandarinus* does not display great outbreaks of numbers. Although it seems to undergo cyclic density fluctuations, their amplitude is comparatively low and the species is never very abundant. Even in optimal habitats the maximal density of burrows does not exceed 5–7 per hectare (DMITRIEV 1980). The reproductive potential of the mandarin vole is low compared with most other microtines. Mean litter size determined by the number of scars in the uterus was 3.65 (DMITRIEV 1980); the number of embryos in nature averaged 4.4; mean number of newborn in the laboratory was 3.3 (ZORENKO et al. 1994). Gestation is 22–24 days. Pups open their eyes only after 13–16 days and wean around 18–22 days. Females become sexually mature at about 38–45 days, males at 55–60 days (ZORENKO et al. 1994). Thus, this species demonstrates the set of characters associated with K-selection (Mc ARTHUR and WILSON 1967).

Some data on the spatial organisation and group composition obtained during two field seasons were briefly reported earlier (SMORKATCHEVA et al. 1990). The aim of this study is to summarise the information on the mandarin vole social system based on data collected throughout 1986–1993.

Material and methods

Study area

This work was carried out in Selenginski District of Buryatia near Lake Torm, 16 km SWW Selenduma (50°53'N, 106°01'E).

Data are presented for the periods June–July 1986; August–mid September 1990; mid April–late May 1991; June–July 1992, and early August–early September 1993. Additionally, some information on spacing and burrow dynamics was obtained in late September 1986 and in late July 1990. At the beginning of each trapping period one of four areas (8–16 ha) within the gentle slopes was selected. We had to change trapping areas because of asynchronous decreases in number of different local populations separated by steep rocky slopes or agricultural fields. When the density of inhabited burrows was low (0.1–0.2 per ha), it was practically impossible to obtain sufficient amount of data. Thus, the local population with the highest density of burrows was selected. Microrelief and vegetation of these four areas are similar. The steppe community is dominated by *Festuca lenensis* with dispersed *Stellera chamaejasme*, *Artemisia frigida*, *Potentilla acaulis*, *P. tanacetifolia*, *Leontopodium* sp., *Thymus serpyllum*, *Arenaria capillaris*, *Lilium tenuifolium*, *Youngia tenuifolia*, *Veronica incana*, *Rumex acetosella*, *Astragalus* sp., *Oxytropis* sp., etc. Everywhere more or lesser overgrazing results in vegetation impoverishment combined with increase of *Stellera chamaejasme* productivity (GORSHKOVA et al. 1977). In the areas under study its density varied from about 50 up to 150–200 individuals per 100 m².

Field studies

All burrows within the chosen area were marked by stakes. Thereafter, the area was inspected daily (early in the morning or after rain) to reveal fresh mounds and plugs of soil. Every fresh mound was plotted (1:75 or 1:150). In this way the data on dynamics for at least 30 days were obtained for 29 burrows. In addition, four burrows were monitored from the very first mounds and were plotted and measured at different stages of development. All burrows in the area were live-trapped. The traps were slightly buried at the fresh mounded burrow entrances, from two to ten per one burrow and were moved according to the movements of the fresh mounds. Slices of stale bread with sunflower oil were used as bait. The live-traps were checked at 3–4 h intervals from 6 a.m. to 11 p.m. We closed traps during very cold nights in autumn and in spring and during very hot afternoons in summer. When first captured, animals were marked by toe-clippings. At each capture voles were weighed, sexed, notes were taken on molt and sexual condition (vaginal smears were taken in females with open vulva). Most of the animals were released immediately. In the case of death of voles in live-traps they were autopsied in order to obtain additional information on the reproductive organs.

Data analysis

Those voles that weighed more than 26 g and/or had adult fur were classified as adults, the remainder as young. Scrotal males and pregnant, nursing, or perforate females were classified as reproductive, the others considered to be nonreproductive. The age of young was determined by the moult development and weight.

Since the composition of groups did not change significantly through a trapping period, our estimations of group size refer to a given session as a whole. Individuals that were not caught repeatedly were assumed to be residents of those group burrows where they were marked. In doing so it was recognised that for some animals (especially subadult individuals) this assumption is not true, and therefore the values of group size must be somewhat overestimated. When no unmarked voles were caught in a burrow for at least 10 days, it was presumed all residents older than 20 days to be marked and these burrows were considered as completely trapped. To verify this, 4 burrows were excavated at the end of the trapping session; of 9 animals caught by hand when excavating, 8 were marked. During spring (1991) and summer (1986 and 1992) sessions, most of the monitored burrows (22/27) were completely trapped. During fall sessions all members of a family apparently were not marked in any of 16 live-trapped burrows, because after the vegetation of *Stellera* had finished, the trapability of mandarin voles decreased.

Group territory sizes were determined on the basis of fresh mound plotting (25–48 points were obtained for each burrow) for a period of approximately one month.

Demographic background

At live-trapped areas the number of inhabited burrows per ha ranged from 0.7 up to 3.0, i.e. middle-high density in this species. Only during the spring session 1991, a low density (0.2 burrows per ha) population was under study. The mean number of adult females per adult male varied from 1 up to 5, with a mean value being 1.9. The sex ratio among young was near 1:1.

Results

As judged from the trapping data, mandarin voles live in extended family groups. The members of a group occupy the common burrow and are strongly attached to it. Of the 194 marked and repeatedly caught voles 92 % were caught at only one burrow.

Among adults marked throughout the first week of each trapping session, 72 % of males (13 of 18) and 64 % of females (19 of 28) were caught in the same burrow system up to the end of the given session.

Mating system

Of five burrows live-trapped during the spring session of April–May 1991 (the beginning of the reproductive period) three were inhabited by pairs of adults without offspring, one by one female with two young, and one by a single adult male.

At the onset of the reproductive period both polygynous and monogamous groups were present in the population. Of a total of 17 groups completely caught during the summer sessions, 7 (41 %) contained one breeding female, 7 (41 %) contained two breeding females, 2 (12 %) contained four and 1 (6 %) contained five breeding females. The number of breeding females averaged 2.4 ($n = 9$) in 1986 and 1.8 ($n = 8$) in 1992. Each of two excavated burrows inhabited by several reproductive females had only one large nest. Thus, there is evidence of joint rearing of pups. From pooled data of 1986 and 1992, reproductive males were present in 17 burrows of 21 live-trapped and in 15 groups of 17 completely caught. In five burrows “additional” reproductive males were observed. In one case the female changed her mate after the former had died. In three burrows the “additional” males were caught only once and, apparently, were dispersers. Only in one

case two adult males were present in the same burrow simultaneously for at least five days.

Of 16 burrows live-trapped during the autumn sessions (pooled data for 1990 and 1993), in 2, 11, and 3 burrows two, one and no reproductive females were present, respectively. In 5 burrows one adult scrotal male was caught, 8 units did not contain scrotal males. Each of the remaining three groups included two scrotal males, one of which being an adult overwintered individual, and another being a young of this year.

Parent-young relationships and natal dispersal

During the spring trapping period only two young males were caught born approximately at the end of March; in mid-May they lived in the natal burrow with an adult female, apparently their mother.

Already in June two cohorts of young were live-trapped in some of the burrows: individuals born in late April–early May and those born in mid-late May. Simultaneously the newborn pups may be present in nests, as was shown by the subsequent trapping. Of a total of 14 family groups completely trapped by July where young were present, 3 included at least three litters, 9 at least two litters and one at least one litter. For these groups, the mean number of the young known to be present was the same in 1986 and 1992 and consisted of 6.4 individuals.

In August–September the young from the same group usually belonged to the same cohort born in July; the older young voles were caught in only three burrows of 16 live-trapped.

The majority of juveniles marked during the first week of each trapping period at 20–30 days of age were recorded staying at the natal site up to 50–60 days, and some of them even up to 70–80 days (Fig. 1).

All young males ($n = 72$) and most young females (70 of 73) remained nonreproductive while staying in their natal burrows. In late June–mid July 1992 three cases of reproductive activation in young philopatric females were registered: a pregnancy in a female

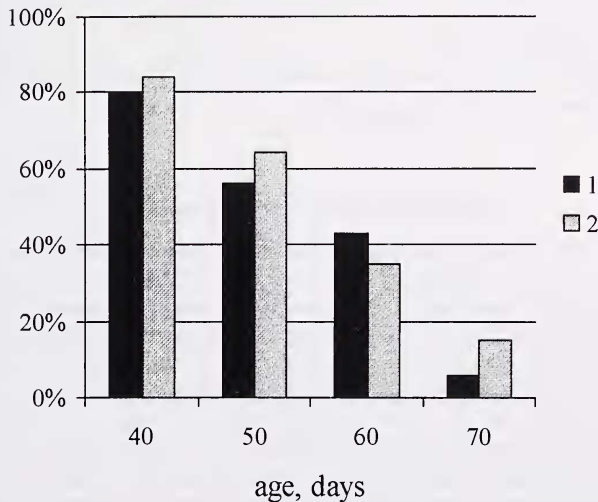


Fig. 1. Proportions of marked juvenile mandarin voles known to remain at natal territory up to the ages of 40, 50, 60, and 70 days. 1-males ($n = 30$), 2-females ($n = 22$).

of about 60 days and the phase of late proestrous-estrous in two females of about 40 days. It is noteworthy that one of the estrous females and the pregnant female were from the same family group, where an old mature female (their mother?) was present and the change of the sire-male occurred.

The composition of groups at the onset of the reproductive period allows to suppose dispersion of young males to be obligatory. Five males marked within natal territories were then captured outside at distances of 20–80 m. Two of them were found in the territories of the adjacent groups, the others at single burrow entrances. They were at an age of 45–75 days when dispersing; all but one were registered as nonscrotal. None of them were caught later. The rather long distance of natal dispersal is likely in these cases because all burrows within a radius of at least 100 m were live-trapped. Besides, 7 unmarked males at the age of 40–60 days were caught (each only once) near single burrow entrances, outside permanent family burrows. These individuals also seem to be dispersers. Two to three voles of the same age were captured at the same entrance, suggesting that they could be littermates.

Concerning the young females, two facts of their resettling in the adjacent burrows (distances 40 and 45 m) were recorded. These individuals were at least 70 days old when dispersing. Both were caught at the new sites as reproductive. Besides, five young females were initially marked in small recent underdeveloped burrows and were most likely among the founders of new breeding units.

All dispersers except one male and one female were registered in late June–mid July.

Size of groups

In spring, at the very beginning of the mass breeding period, all families were small and included 2–3 individuals.

According to the data of 1986 and 1992 for completely trapped burrows, in June–July the average social group contained 9.4 ($n = 9$) and 8.0 ($n = 8$) individuals, respectively. By July 1986 the number in one of the families reached 22 individuals; afterwards this family and group burrow gradually divided into two. The former mature male remained in one part, the new unrelated male appeared in another. The formation of new families was observed in early July 1986 (2 groups) and mid-July 1992 (1 group). From the very beginning, each of them consisted of one male with two females. Among the founders were both young and adult individuals.

During the late summer-fall the mean number of individuals caught per burrow was 3.47 and 3.72 in 1990 and 1993, respectively.

Spacing and territorial relationships

In *L. mandarinus* the density of inhabited burrows is comparatively low; the nearest ones usually are separated by a distance of several dozens of meters. Although this space is often holed by the set of destroyed or left tunnels, it seems to prevent a direct contact between the resident individuals from distant groups. Occasionally burrow-clusters were observed, several group territories being located close to each other (Fig. 2). In such cases burrow systems of different family groups were not connected by tunnels. Members of a certain group normally did not visit strange burrows. During 5 trapping sessions only 9 marked voles were observed to intrude. Among them, 4 individuals (2 young males and 2 young females) most likely were dispersers. Three voles (one adult female and two adult males) lost their mates and were probably looking for new ones. The remaining two voles were a pair occupying an adjacent burrow, of which hosts had disappeared two weeks before.

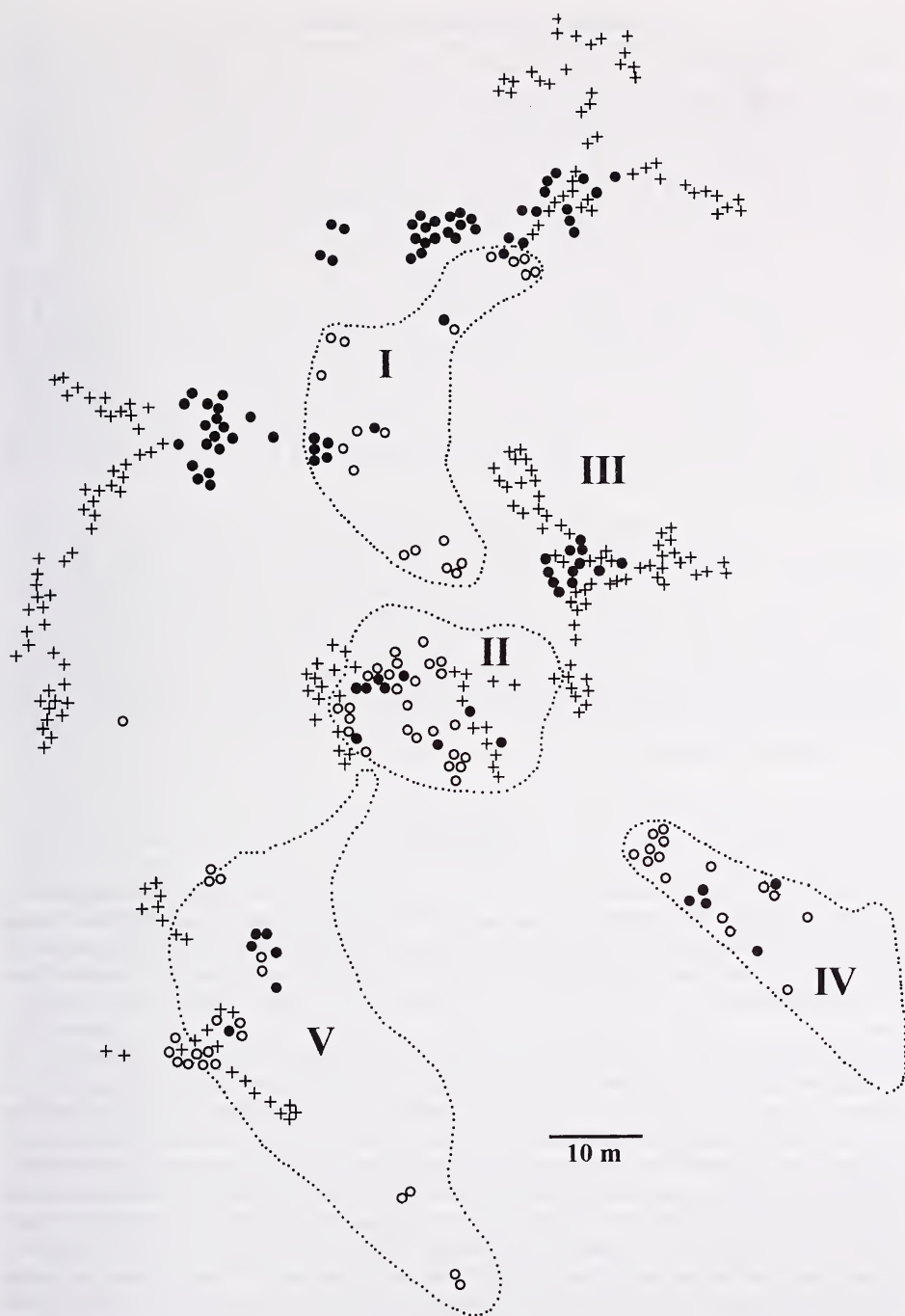


Fig. 2. Dynamics of five mandarin vole burrows (June–July, late September 1986) as revealed by soil mounds. Dashed lines indicate areas covered by old mounds in early June. Open circles, solid circles, and crosses indicate new mounds plotted in June, July, and September, respectively.

Group territory sizes and dynamics

At the very beginning of the spring trapping session (mid-April 1991) most part of the area under study was covered with mounds of soil indicating that many burrows were inhabited in March. For 20 well-distinguishable burrows the mean size (\pm SE) determined by the old mounds was $265 \pm 55.9 \text{ m}^2$. However, the following observation revealed only 4 burrows where the fresh mounds had appeared; their areas determined by the mounds registered from 20 April up to 20 May were 110 m^2 (inhabited by a single female with young), 70, 15, and 25 m^2 (each inhabited by a pair of adults). The fifth burrow was founded by a single male in early May and reached 25 m^2 by 20 May.

During the summer sessions of 1986 and 1992, a total of 14 burrows were followed through at least one month, most of them from the first decade of June up to the first decade in July. For this period, the mean size (\pm SE) of the burrows consisted of $142 \pm 32.4 \text{ m}^2$ (range $50\text{--}370 \text{ m}^2$, $n = 13$, pooled data of 1986 and 1992). The fourteenth burrow was extremely large; by July it reached about 600 m^2 (this value is not included in the calculation) with the family consisting of 22 individuals. In late July this family had divided into two, which began to exploit the different parts of the enormous territory. By October these burrows were separated from one another by a distance of over 40 m (Fig. 2, burrow I).

In early-mid July the dispersal of young was attended by the emergence of new small burrows (e.g., burrow III, Fig. 2). Three burrows that were monitored from the first mounds grew very rapidly: within two weeks they reached 15, 15, and 54 m^2 . By late September the soil mounds in smaller burrows covered areas of 112 and 140 m^2 (1986).

In late summer-late autumn a considerable increase of the burrowing activity was observed. During fall daily 3–6 (up to 12) fresh mounds per burrow were recorded, e.g. equivalent to only 1–3 (up to 6) mounds per burrow in summer. An area exploited by a family group from mid-August up to mid-September 1993 averaged (\pm SE) $177 \pm 32.0 \text{ m}^2$ ($n = 11$), range $80\text{--}330 \text{ m}^2$.

Discussion

From the trapping data results, the basic type of spatial organisation for *L. mandarinus* is group territoriality. The mating system varies from polygyny to monogamy, the former predominating. Mateships are prolonged and appear to dissolute if some of the mates die. Young born in spring as well as later stay with their parents for a long time. As has been shown in the laboratory (ZORENKO et al. 1994; SMORKATCHEVA et al. 1997), the life cycle of *L. mandarinus* is characterized by rather long intervals between weaning (about 19–22 days) and the earliest age of fertility (55–60 days for males, 36–38 days for females). In this study most of the young were known to remain in their natal burrows during this ontogenetic phase. Apparently, they help their mother rear subsequent 1–2 litters both by direct and indirect parental investment as it was observed in the laboratory (ZORENKO et al. 1994). For reproduction, sons apparently must leave the natal territory. According to trapping data young males seem to disperse at the age of 45–70 days, i.e. about the time of puberty. Daughters may stay in the natal territory as nonreproductive female, stay and reproduce, or disperse. In contrast to males no young female was recorded as migrant, although two individuals were known to settle at new sites. Several females were captured in their natal burrow as reproductive. *L. mandarinus* display strong incest-avoidance and contact with strange male is necessary for reproductive activation of young females (SMORKATCHEVA et al. 1997). Evidently females wait for a mate in their natal territory for some time after becoming physiologically fertile. Meanwhile, they increase their inclusive fitness by helping kin individuals and receive a chance to inherit the parental burrow and

territory thereby, avoiding risks involved in dispersal. The change of sire appears to be the necessary condition to realise this chance. Most of polygynous groups are likely formed in such a way.

The question remains open about the proximate causes of natal dispersal in *L. mandarinus*. From our preliminary laboratory data only amicable interactions occur between family members independent of their age. These observations do not support the hypothesis that aggression from adult members of the group forces the young to disperse (CHRISTIAN 1970; ANDERSON 1980; BOONSTRA et al. 1987). It is more probable that different factors trigger the dispersal in the two sexes. Internal physiological cues might be sufficient to promote male dispersal. In female ontogeny not the "dispersal phase", but the "mating or waiting for a mate phase" seems to be present. Natal dispersal of females was shown to be preceded by maturation and mating in *M. arvalis* (BOYCE and BOYCE 1988). Hormonal events induced by copulation probably account for strong female bonding to male in monogamous *M. ochrogaster* (CARTER and GETZ 1993). In the latter species, the important role of non-resident, non-paired males in reproductive activation of young females was clearly demonstrated (CARTER et al. 1980; MCGUIRE and GETZ 1991; MCGUIRE et al. 1990; LYONS and GETZ 1993). For *L. mandarinus*, I hypothesise that not only non-resident males activate the reproduction, but also may promote the dispersal of young females if their mate does not remain with their family after copulation.

If this hypothesis is true the following predictions should be realised:

(i) the higher the number of non-paired males in a population, the greater the proportion of young females becoming reproductive

(ii) the higher the mortality in fathers, the greater the proportion of daughters reproducing within the natal territory.

Thus, (iii) if the survival of mated males is high and numerous unmated males are present in a population, then high levels of female natal dispersal and increasing numbers of new breeding units should be expected.

These assumptions should be examined both in field demographic studies and in laboratory ethology experiments.

Thus, in nature *L. mandarinus* exhibits group territoriality, prolonged pair-bonding, and parent-young relationships. Previously the species was reported to display the characters of K-strategy (small litter size, slow development and sexual maturity, incest-taboo), paternal care activity, care by weaned young of pups, long latency, and low level of copulatory stimulation (ZORENKO et al. 1994; SMORKATCHEVA 1997). All of these traits are usually attributed to monogamy (KLEIMAN 1977; DEWSBURY 1990). However, *L. mandarinus* combines a monogamous system of rearing with a polygynous system of grouping and mating. It is this combination of traits that underlies the high level of sociality in the mandarin vole.

The social structure of this species appears to be similar to that of the prairie vole *M. ochrogaster* and the pine vole *M. pinetorum*. The latter two species are the classical examples of monogamous microtines, although both display communal reproduction under certain conditions as well (GAVISH et al. 1981; FITZGERALD and MADISON 1983; GETZ et al. 1990). The tendency of the young to philopatry and cooperative breeding has been found in the prairie vole (MCGUIRE et al. 1993) as well as in the pine vole (FITZGERALD and MADISON 1983). These examples of monogamous or communal breeding units in voles are often considered to be exceptional (e.g. ANDERSON 1980; WOLFF 1985; NELSON 1987). However, the analysis of the available data dealing with the spatio-social structure for Old World microtines shows that this pattern is not at all that rare. Apparently, it is typical for *Microtus socialis* (SHCHIPANOV and KASATKIN 1996), *Eolagurus luteus* (LABUNETZ 1968; SHUBIN 1974), *Prometheomys schaposchnikovi* (GAMBARYAN et al. 1957; TUROV 1926), *Laopiopodmys brandti* (KHRUSTZELEVSKI 1954 a; GROSSE et al. 1984; DMITRIEV et al. 1992; XIN-RONG et al. 1998), and *Ellobius talpinus* (SHUBIN 1961; ZUBKO and OSTRYAKOV 1961).

The mating system of *M. ochrogaster* is generally believed to be an adaptation to homogeneous, stable, low-food habitats where the females are widely dispersed and it is better for a male to guard a selected mate instead of searching for others (GETZ 1978; NELSON 1987; GETZ and CARTER 1996). However, the benefits associated with living in groups are unclear for this species (GETZ et al. 1990; MCGUIRE and GETZ 1995). In *M. pinetorum* and *L. mandarinus* it is the fossorial habits that might explain prolonged pair-bonding as well as phylopatriy and sociality if we presume that:

- (i) the risk of above-ground wandering is especially high for the fossorial animals;
- (ii) the construction of new tunnels is also associated with high costs (POWELL and FRIED 1992);

- (iii) the male and the philopatric offspring gain indirect fitness benefits by forage tunnel building and maintenance and probably care for pups (POWELL and FRIED 1992).

However, the statement of ELWOOD (1983) that direct care of offspring (huddling, grooming, retrieving) by a male is rather a result of his staying with the mother appears to be likely for voles.

Thus, the set of traits mentioned above (prolonged strong pair-bonding, retention by mature offspring, care of the offspring by all group members) is not specific only for fossorial microtines but is expected to be typical for all of them. It seems to be true for a few species other than *M. pinetorum* and *L. mandarinus*, whose social pattern has been reported, *Prometheomys schaposchnikovi* (TUROV 1926) and *Ellobius talpinus* (SHUBIN 1961; ZUBKO and OSTRYAKOV 1961).

When the group composition of *L. mandarinus* is compared with that of other social microtines, the former appears to resemble most closely *L. brandti* by the complexity and large size of units. In both species the summer groups consist of 6–8 individuals (up to 20–25) and often include several reproductive females and 2–3 generations of young; the division of oversize families into several distinct ones has been described previously (GROSSE et al. 1984; DMITRIEV et al. 1992; XIN-RONG et al. 1998; this study). In contrast to this, the social groups generally contain 2–3 reproductive animals with only a few offspring in *Microtus socialis* (SHCHIPANOV and KASATKIN 1996), *M. ochrogaster* (GETZ et al. 1993), *M. pinetorum* (FITZGERALD and MADISON 1980), and *Eolagurus luteus* (SHUBIN 1974). The analysis of data available on sexual maturity in voles reveals a second trait that *L. mandarinus* and *L. brandti* have in common. This is the great obligatory delay of fertility with respect to weaning. In *Lasiopodomys* the minimal age of fertility in females has been reported as 35–40 days (*L. mandarinus* see ZORENKO et al. 1994; *L. brandti* see ZORENKO and JAKOBSONE 1986), males maturing even later. This phase of ontogeny may be considered as “period of helping”. In most studied microtines from grasslands, both the delay of maturation and dispersal are facultative with the earliest conceptions in females occurring at about weaning or soon after, at 15–30 days (POKROVSKI 1967; SHUBIN 1974; NADEAU 1985; BOYCE and BOYCE 1988). The exceptions are *M. pinetorum* (SCHADLER and BUTTERSTEIN 1979) and probably, *Ellobius talpinus* (ZUBKO and OSTRYAKOV 1961).

Finally, the third trait of *Lasiopodomys* apparently associated with a high level of sociality, is the predominance of tactile contacts during interactions of these voles.

Thus, the genus *Lasiopodomys* seems to be among the most social of voles. The genus now occurs in the open, highly seasonal grasslands of Central Asia. The colonial organisation of *L. brandti* is thought to be associated with (1) construction of complex by extended winter burrows, (2) storage of winter-food supplies in snow-free steppe, and (3) use of acoustic communication like ground squirrels to avoid predators (NAUMOV 1955; NIKOLSKI 1979; GROSSE et al. 1984). The mandarine vole has solved both the problem of predators and that of winter storage by the transition to subterranean existence and foraging. Moreover, the northern subspecies *L. mandarinus vinogradovi* presents an exceptional example of the tendency towards monophagy, that is rare among voles (the only known monophagous species is *M. breweri*, ROTHSTEIN and TAMARIN 1977) as well as

among the fossorial mammals (ORLOV 1978; NEVO 1995). At the same time, neither its appearance nor its skull and bones of the extremities seem to demonstrate significant morphological adaptations to a fossorial mode of life. It can be hypothesized that the high level of sociality was characteristic of the ancestral above the ground form and represented the precondition to occupy the recent niche. Probably it is the collective tunnel construction that allows the mandarin voles to feed on the dispersed large roots, as is accepted for mole-rats Bathyergidae (JARVIS 1981; LOVEGROVE and WISSEL 1988).

Acknowledgements

I thank EKATHERINE TSYTSULINA for her assistance in the field and am also grateful to Dr. NATALIA AMBRAMSON for reviewing the English version of the manuscript.

Zusammenfassung

Soziale Organisation der Mandarin-Wühlmaus (Lasiopodomys mandarinus) während der Reproduktionsperiode

Das Sozialsystem in freilebenden Populationen von *Lasiopodomys mandarinus* wurde im Selenginski Distrikt in Burjatien mit Markierungs-Wiederfang-Methoden untersucht. Mandarin-Wühlmäuse lebten in umfangreichen Familiengruppen. Die Mitglieder einer Gruppe waren streng an einen gemeinsamen Bau gebunden. Die Gruppen bestanden im Sommer aus einem reproduzierenden Männchen, 1–5 reproduzierenden Weibchen und von 1–3 Generationen von Jungtieren; durchschnittlich fanden sich 8,7 Individuen pro Bau (Umfang 3 bis 22). Die meisten Nachkommen blieben im Elternterritorium wenigstens 50 Tage lang. Keines von 72 jungen Männchen und nur drei von 73 jungen Weibchen begannen sich im Geburtsbau zu vermehren. Der Wechsel des Vattertieres ist wahrscheinlich eine wichtige Bedingung für die reproduktive Aktivierung von philopatrischen Töchtern.

Folglich zeigt *L. mandarinus* einen hohen Grad an Sozialität, der auf gemeinsamer Jungenpflege und verlängerten Paarbindungen sowie auf verlängerten Bindungen zwischen Eltern und Jungtieren begründet ist. Diese Merkmale werden in der Literatur auch für die Art *Lasiopodomys brandtii* beschrieben. Vermutlich war diese soziale Organisation für die nicht subterrane Anzestralform der beiden Arten typisch und die Voraussetzungen dafür, die Nische eines unterirdischen *Stenophagen* zu besetzen.

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